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INFLUENCE OF SINGLE TREES ON FLORISTIC DIVERSITY OF STEPPE MEADOWS AND POPULATION STRUCTURE OF SOME RARE PLANT SPECIES

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In the zone of broad-leaved forests of the European Russia, steppe meadows have been preserved showing rich floristic composition and making a significant contribution to the biological diversity of the territories. Bryansk oblast is one of the forest regions in Russia where such meadows are found. Here, steppe meadows with high floristic diversity and a large number of rare plant species have survived. Trees from surrounding forest areas are constantly encroaching on these meadows. Most of the young trees die from regular grass fires and economic activity. However, some individuals survive and reach a generative state, becoming relatively resistant to ground fires. The influence of single trees on the floristic diversity of steppe meadows was studied at two levels of living system organization – coenotic and population levels. Polydominant steppe meadows and polydominant steppe meadows with single generative trees were studied at the coenotic level; and coenopopulations of *Iris aphylla*, *Anemone sylvestris*, and *Anthericum ramosum* were studied at the population level. Collecting the material, we used different methods: geobotanical, demographic, and measurements of environmental factors (illumination, slope steepness, and the frequency of grass fires). Polydominant steppe meadows were found to be preserved in the middle part of steep slopes unsuitable for haymaking and grazing and subjected to infrequent grass fires. These communities have high floristic diversity and stable coenopopulations of model species. Ontogenetic spectra of *Anemone sylvestris*, *Anthericum ramosum*, and *Iris aphylla* are of the complete left-hand type with the maximum number of individuals. Single trees (*Quercus robur*, *Tilia cordata*) have controversial influence on the vegetation of polydominant steppe meadows. On the one hand, with the introduction of trees, species diversity of communities increases. This is due to the fact that trees offer resting places and shelter for birds that spread plant diaspores. On the other hand, mature trees shade the herb cover. This leads to cover reduction and occurrence of steppe and dry meadow species, as well as affects their population structure. The ontogenetic spectrum of *Anemone sylvestris* is still complete, whereas that of *Iris aphylla* becomes incomplete, and the spectrum of *Anthericum ramosum* becomes unfinished.

Key words: *steppe meadow, single trees, floristic diversity, coenopopulations, ontogenetic spectrum, state of coenopopulations, Anemone sylvestris, Anthericum ramosum, Iris aphylla*

Steppe meadows have survived in the zone of broad-leaved forests of the European Russia (Bulohov, 1977, 2001; Bosek, 1980; Skvorcov, 1982; Averinova, 2010; Semenishhenkov, 2010, 2012; Evstigneev et

al., 2011; Panasenko et al., 2013, 2015, etc.). These communities, in general, have rich floristic composition and make a significant contribution to the biological diversity of the territories. However, due to human economic

activity and grass fires, such coenoses are in danger of extinction (Zelenaja ..., 2012; Evstigneev et al., 2018a; Ruchinskaya, 2019). Woody plants from the surrounding forest areas are constantly encroaching on the steppe meadows preserved in the zone of broad-leaved forests. Most of the young trees die from regular grass fires and economic activities such as haymaking, grazing, etc. However, some individuals survive and go into a generative state (Evstigneev et al., 2018a). Mature trees are relatively resistant to ground fires: their renewal buds are located high and the thick crust of the trunk protects the cambium (Serebrjakov, 1962). Single trees affect the growing conditions of other plants in the meadows. It is known that in phytogeneous fields of trees, illumination, air temperature and humidity, soil temperature and humidity, the amount of precipitation penetrating through the crown, quality of litter, concentration of nutrients and other soil characteristics change significantly (Uranov, 1965; Samojlov, 1983; Nikonov et al., 2002; Ipatov, 2007; Zhuravleva et al., 2012; Orlova et al., 2016). In addition, single trees attract animals of different ecological groups, e.g. soil invertebrates, mouse-like rodents, birds, etc. (Manning et al., 2006; Prevedello et al., 2018). On the one hand, these influence the

growing conditions of plants, and on the other hand, they participate in the creation of both intracoenotic and intercoenotic flows of diaspores. Therefore, the objective of this work is to consider the influence of single trees on the floristic composition and the state of coenopopulations of some rare plant species in the steppe meadows.

MATERIAL AND METHODS

The research was carried out in the south-east of Bryansk oblast within the Melovitskie Slopes natural monument (Figure 1). The site is located in Komarichsky-Sevsky physiographic region. It consists of elevated loess plains with ravines, gullies, slopes and outcrops of carbonate rocks on the western offsets of the Central Russian Upland. Botanically and geographically, the territory belongs to the Eastern European Province of the European broad-leaved forest region (Rastitel'nost'..., 1980). Komarichsky-Sevsky district has temperate continental climate. The mean annual temperature is 5.4 C. The duration of the warm season with above-freezing temperatures is 228 days; the growing season with the temperature above + 5°C is 188 days. Mean annual precipitation is 613 mm; the mean precipitation in the warm season is 342 mm (Prirodnoe ..., 1975).

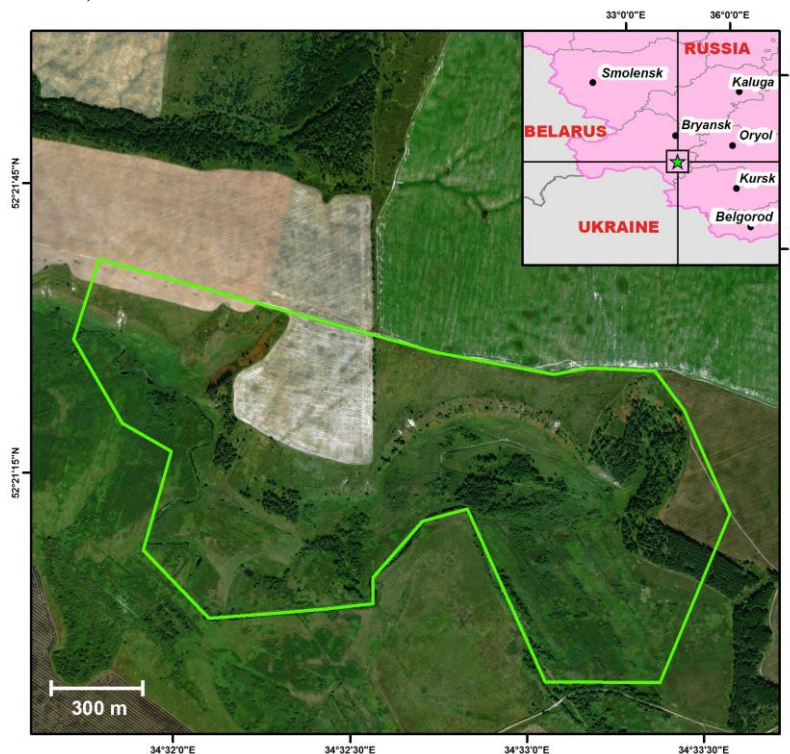


Figure 1. Location of the Melovitskie Slopes natural monument. The green line represents the boundaries of the research object. Background satellite imagery by Microsoft Bing Maps

The research was carried out at two levels of living system organization, i.e. at the coenotic and population level. Polydominant steppe meadows and polydominant steppe meadows with single generative trees were studied at the coenotic level. At the population level, the objects of the study were coenopopulations of model plant species *Iris aphylla* L., *Anemone sylvestris* L., and *Anthericum ramosum* L. *Iris aphylla* is a short rhizome rosette spring-flowering summer-green plant (Figure 2, A). It is a geophyte. *Anemone sylvestris* is a perennial herbaceous spring-flowering summer-green short rhizome plant (Figure 2, B). It is a hemicryptophyte and geophyte. *Anthericum ramosum* is a perennial herbaceous summer-green summer-flowering short rhizome plant (Figure 3). It is a hemicryptophyte and geophyte. These species were chosen due to the fact that they are rare, endangered and listed in Red Books of many regions (Krasnaja..., 2002, 2004, 2015, 2016, etc.). Moreover, *Iris aphylla* is listed in the Red Book of Russia (2008).

The following research methods were used: geobotanical, demographic, statistical, and measurements of habitat factors. Relevés were made on plots of 100 m² in 11-fold repetition for each community type. A complete floristic list was compiled at each plot. Species participation was evaluated as scores according to the cover-abundance scale proposed by J. Braun-Blanquet (Mirkin et al., 1989). Species richness and species density were used to assess the species diversity of communities. Species richness is the total number of species in a community, which is obtained on the basis of 11 relevés. Species density is the average number of species per unit area. The names of vascular plants were given according to The Plant List international database (<http://www.theplantlist.org/>). For relevé analysis of communities, ordination was carried out using Detrended Correspondence Analysis (DCA). This method works successfully with heterogeneous data of relevés (Dzhongman et al., 1999). PC-ORD software was used for calculations. Demographic research was based on ontogenesis periodization proposed by T.A. Rabotnov (1950) and supplemented by A.A. Uranov (1975) and other scientists

(Cenopuljicii ..., 1988). Ontogenesis is divided into stages that show morphological and functional differences. Individuals belonging to the same ontogenetic state are grouped together: *j* – juvenile, *im* – immature, *v* – virginile, *g₁* – young generative, *g₂* – mature generative, *g₃* – old generative, *ss* – sub-senile, *s* – senile. Ontogenetic states of the model species were determined on the basis of publications (Evstigneev et al., 2018; Ruchinskaya, 2019). The state of coenopopulations was estimated using the number, density, and type of the ontogenetic spectrum. Number is the number of individuals in the study area (Chernova, Bylova, 2007). Population density is the average number of individuals per unit area (Odum, 1986; Cenopuljicii ..., 1988). The type of the ontogenetic spectrum was named according to the classification proposed earlier (Zaugol'nova, 1994b). In the meadows and under the trees, the illuminance was measured hourly with a light meter on a cloudless June day from 10 a.m. to 6 p.m. Illuminance in lux was converted to a percentage of the total illuminance, which was measured in the open space. The slope steepness was measured using a Nikon Forestry Pro rangefinder. The frequency of grass fires was determined by the age of shoots of formation in shrubs (*Frangula alnus* Mill., *Corylus avellana* L.). These shoots emerge from dormant buds located in the basal part of the shrub. The former aboveground shoots were destroyed due to fire damage (Figure 4).

RESULTS AND DISCUSSION

Polydominant steppe meadows were preserved in the middle part of steep slopes hardly suitable for haymaking and grazing (Figure 5). Grass fires mainly occur once every two years. They limit the introduction of woody plants as young tree species are most vulnerable. For instance, seedlings and juvenile oak plants often die during grass fires (Komarov, 1951). As a result, polydominant communities with high species diversity are formed (Table 1; Suppl. materials). These coenoses are unique since they include species that are characteristic of steppe communities: *Ajuga genevensis* L., *Anemone sylvestris*, *Aster amellus* L., *Astragalus cicer*

L., *Campanula sibirica* L., *Prunus cerasus* L., *Galium tinctorium* L., *G. verum* L. etc. The ecological-coenotic structure is dominated by plants of the dry meadow group, which also includes the above-named steppe plants. Moist meadow (*Festuca pratensis* Huds., *Hypericum maculatum* Crantz, *Succisa pratensis* Moench, *Thalictrum lucidum* L. и др.), nemoral forest-edge (*Brachypodium pinnatum* (L.) Beauv., *Peucedanum cervaria* (L.) Cusson ex Lapeyr, *Laserpitium latifolium* L., *Lathyrus pisiformis* L., *L. sylvestris* L., *Pyrethrum corymbosum* (L.) Scop.), and nitrophilous forest-edge (*Rubus caesius* L.

and *Valeriana officinalis* L.) plants are often found as well. Small participation is typical of forest species, i. e. nemoral – *Convallaria majalis* L., *Corylus avellana*, *Quercus robur* L., *Viola mirabilis* L., boreal – *Frangula alnus*, and piny – *Pteridium aquilinum*, *Solidago virgaurea* L., and *Viola collina* Besser. Diaspores of forest and forest-edge species are brought here by animals and wind from the neighbouring pine forest. Moist meadow and nitrophilous species are brought from floodplain communities adjacent to the slope.

Table 1. Characteristics of communities on the steppe slopes. Melovitskie Slopes natural monument

Indicators	Communities	
	1	2
Slope angle		
Slope angle, $M \pm \sigma$	37 ± 2.4	31 ± 2.4
Slope angle range	33–41	28–37
Number of measurements	21	33
Fires		
Fire frequency, $M \pm \sigma$	2.3 ± 1.2	2.2 ± 1.0
Number of measurements	52	33
Characteristics of the diversity of vascular plant species		
Average number of species per 100 m ² , $M \pm m_M$	51 ± 1.2	59 ± 1.2
Range of number of species per 100 m ²	44–56	52–66
Number of species on 11 plots of 100 m ² each	98	107
Number and proportion (%) of species of different ecological-coenotic groups		
Dry meadow	77 (78.6)	79 (73.8)
Moist meadow	5 (5.1)	7 (6.5)
Nemoral forest	4 (4.1)	8 (7.5)
Nemoral forest-edge	6 (6.1)	6 (5.6)
Piny	3 (3.1)	3 (2.8)
Boreal forest	1 (1.0)	1 (1.0)
Nitrophilous forest-edge	2 (2.0)	3 (2.8)

Note. M is the arithmetic mean, and σ is the standard deviation. Communities: 1 – polydominant steppe meadows, 2 – polydominant steppe meadows with single generative trees

Iris aphylla is one of the predominant species in the herb layer of polydominant steppe meadows of the Melovitskie Slopes. Population density of *Iris aphylla* is 82 plants per 1 m². The ontogenetic spectrum is complete single-peak with a maximum at v and g_n plants (Figure 6, 1a). *Iris aphylla* is well adapted to high illuminance of open spaces due to the structure of its leaves: they are flattened laterally and vertically oriented (Evstigneev et al., 2018b). Seed renewal of *Iris aphylla* is facilitated by the activity of

animals such as ants and mouse-like rodents that inhabit the slopes and create disturbances. These microsites are characterized by sparse herb cover, loosened substrate, increased aeration and soil temperature, and significant microbiological activity (Zrjanin, 2003; Dauber, Wolters, 2000; Kostrakiewicz, 2004, etc.). For example, a population locus consisting of 10 juvenile plants was found in a 0.03 m² earth ejections of the mouse-like rodent. The spread of *Iris aphylla* diaspores is facilitated by ants (Figure 7). R.E. Levina

(1957) states that fresh seeds attract these animals with sweet, sticky liquid that is contained in the shell. Our observations

showed that ants also spread dry seeds (Evstigneev et al., 2018b).



Figure 2. Model plants species in steppe meadows of the Melovitskie Slopes natural monument: *A* – *Iris aphylla*, *B* – *Anemone sylvestris*. Photo by A.V. Gornov



Figure 3. Model plants species in steppe meadows of the Melovitskie Slopes natural monument:
A, B – Anthericum ramosum. Photo by E.V. Ruchinskaya

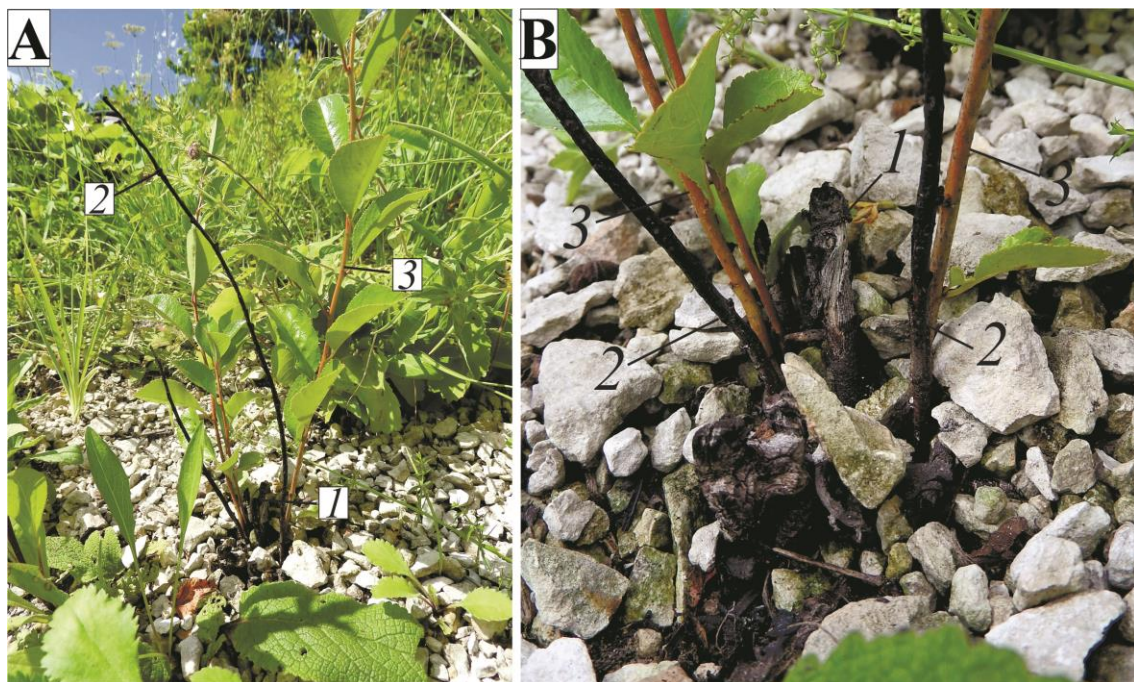


Figure 4. Coppice shoots of burnt sour cherry (*Prunus cerasus*).
 A – general appearance of the shrub, B – base of the shrub. 1 – stump of a burnt perennial shoot, 2 – dead burnt biennial coppice shoot, 3 – live annual shoot that woke up from a dormant bud after a ground fire in the spring (from: Ruchinskaya, 2019)



Figure 5. Polydominant steppe meadows in the territory of the Melovitskie Slopes natural monument. Photo by A.V. Gornov

Anthericum ramosum is a codominant species in the herb layer of steppe meadows. Population density of *Anthericum ramosum* is 56 plants per 1 m². Ontogenetic spectrum is complete, left-hand type, single-peak with a maximum at v and g_h plants (Figure 6, 2a). The formation of the maximum at v and g_h plants is determined by the following: 1) short duration of j and im states; 2) recruitment of plants resting from flowering; 3) recruitment of v with plants of vegetative origin formed as a result of disintegration of g_2 plants.

Anemone sylvestris can be both an associate and a codominant in the herb layer of steppe meadows. Population density of *A. sylvestris* is 75 plants per 1 m². Ontogenetic spectrum is complete left-hand type with a maximum at im plants (Figure 6, 3a), the density of which is 27 trees per 1 m². No *A. sylvestris* individuals of seed origin were found in the studied community. Therefore, the spectrum can be called vegetative and complete. High population density and the complete ontogenetic spectrum are determined by the

biology of *A. sylvestris*. Large number of plants of the pregenerative state is due to the ability of *A. sylvestris* to vegetative reproduction with deep rejuvenation (Figure 8). Vegetative individuals develop from buds that appear on horizontal adventitious roots (Starostenkova, 1986; Barykina, Potapova, 1994). The beginning of the growth season in early spring, before the herb layer rises,

contributes to the accumulation of a sufficient amount of macronutrients required for the formation of generative organs in plans. It is worth noting that the absence of seed individuals is evidence of adverse conditions for the coenopopulation. Apparently, this is due to the spread of fire on the slopes, which destroys young seed individuals of *A. sylvestris*.

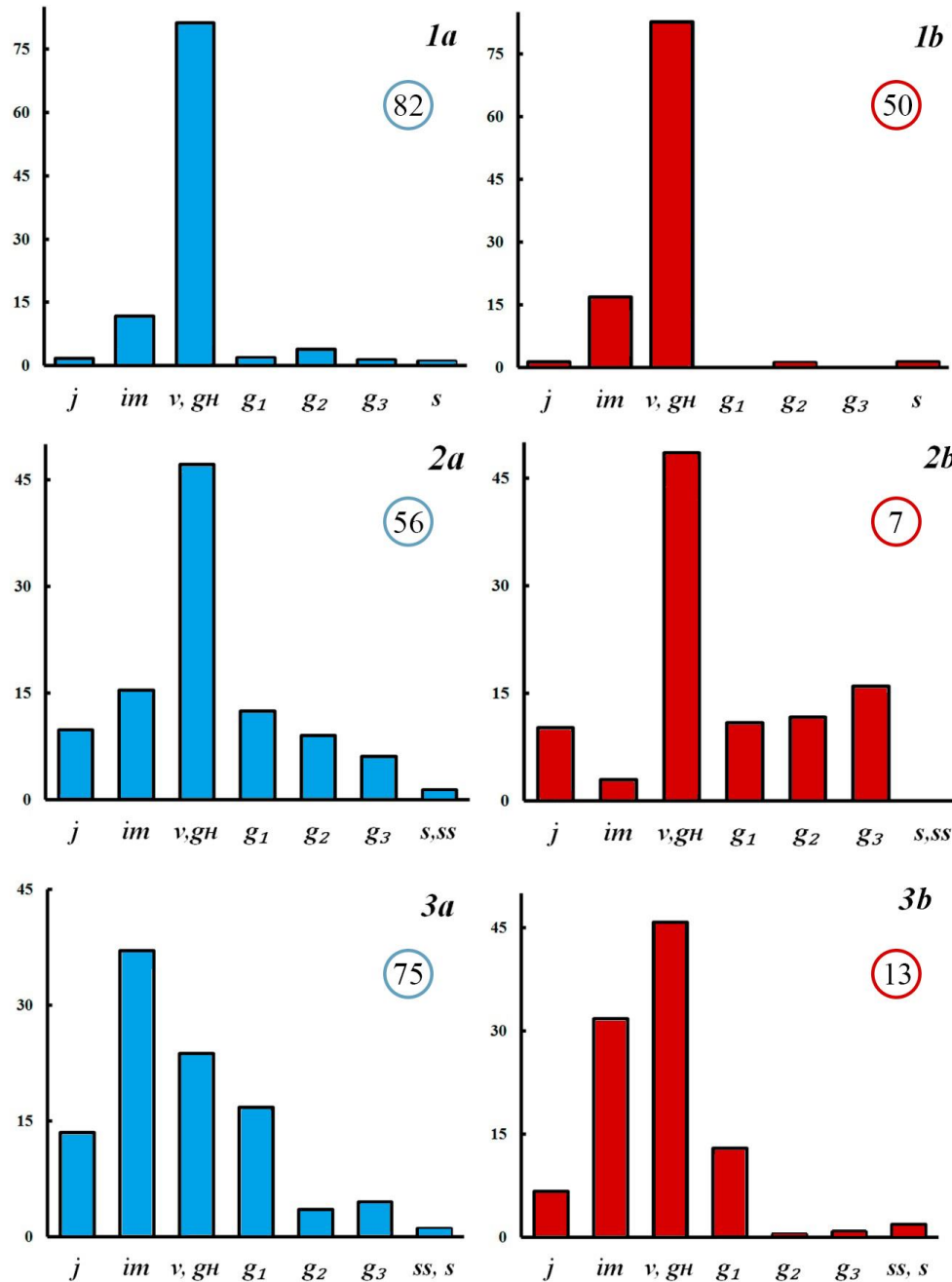


Figure 6. Ontogenetic spectrum of coenopopulations of model plant species in steppe meadows. 1 – *Iris aphylla*, 2 – *Anthericum ramosum*, 3 – *Anemone sylvestris*. The X axis shows ontogenetic states, and the Y axis – the proportion of individual plants, %. Circled is population density (the number of plants per 1 m²) is shown. Communities: a – polydominant steppe meadows, b – polydominant steppe meadows with single generative trees. Ontogenetic states of trees: j – juvenile, im – immature, v – virginile, g_n – temporarily not flowering generative plant, g₁ – young generative, g₂ – mature generative, g₃ – old generative, ss – subsenile, s – senile



Figure 7. Dispersal of fresh *Iris aphylla* seeds by the red forest ant (*Formica rufa*).
Photo by E.V. Ruchinskaya

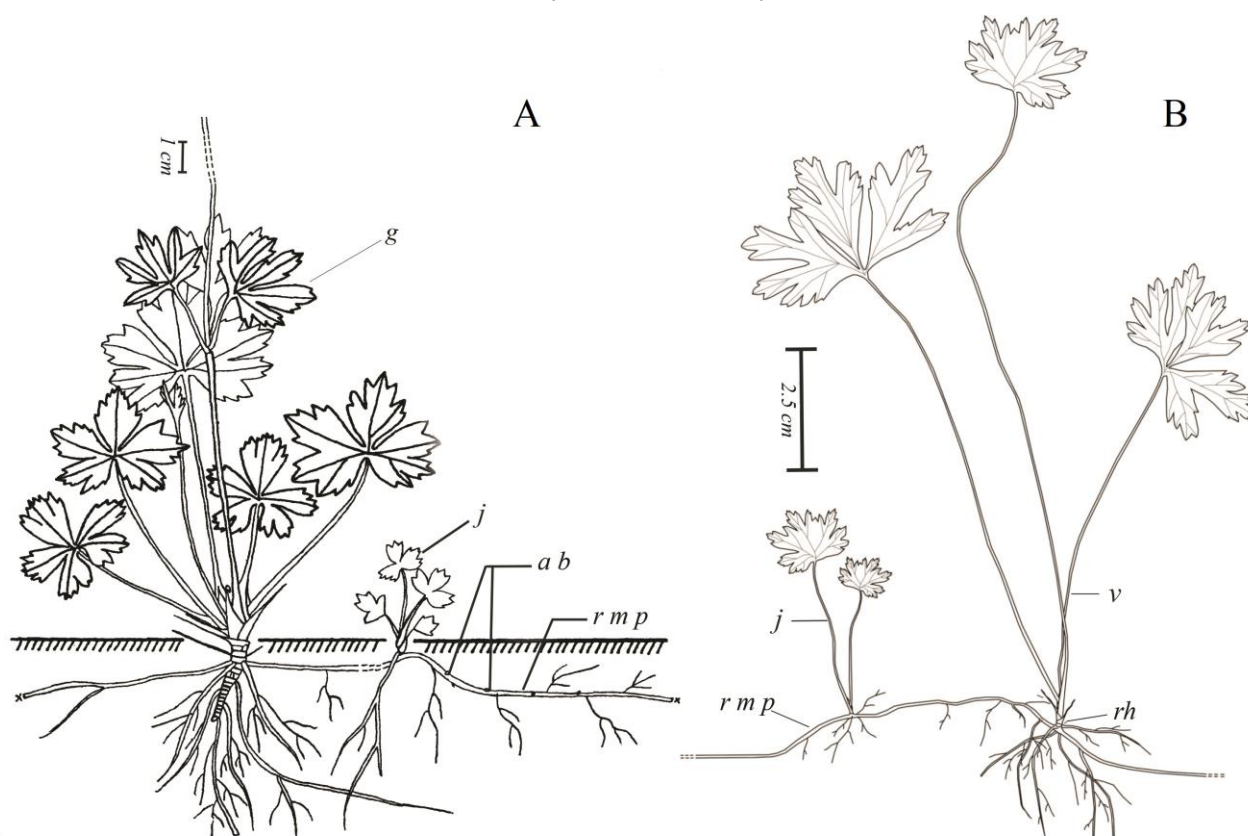


Figure 8. Vegetative renewal of *Anemone sylvestris*: A – generative individual with a root shoot and adventitious buds on the root (from: Barykina, Potapova, 1994, as supplemented), B – juvenile and virginal individuals of root shoot origin (from: Gornov et al., 2013). *j* – juvenile individual, *g* – generative individual, *v* – virginal individual, *rmp* – root of the parent plant, *rh* – rhizome, *ab* – adventitious bud

Polydominant steppe meadows with single generative trees. On the slopes, there are single *Quercus robur* and *Tilia cordata* generative trees (Figure 9), which survived fire during their virginile stage. Mature oaks and linden trees are relatively resistant to ground fires: their renewal buds are located high, and the thick crust of the trunk protects the cambium (Serebrjakov, 1962). The steepness of the slope and the frequency of grass fires are similar to polydominant steppe meadows. Ordination of relevés divided polydominant steppe meadows and polydominant steppe meadows with single trees into distinct groups (Figure 10). The communities differ in the maximum values of species richness and species density (Table 1; Suppl. materials). High species diversity is due to several factors. First, in the past, the communities were not subjected to active grazing or haymaking, as they are also located on steep parts of the slopes. Second, single trees offer resting places and shelter for many animals, including birds. These are known to disperse seeds of meadow and forest plants (Manning et al., 2006; Prevedello et al., 2018). As a result, communities with free-standing trees have higher species richness than polydominant steppe meadows. The ecological-coenotic structure of the community is dominated by dry meadow and steppe plants. Under the crowns of single trees, the illuminance is reduced to 60% of the total. Shading reduces the cover of light-loving dry meadow and steppe plants. However, the number of species in this group increases. *Allium oleraceum* L., *Artemisia absinthium* L., *Carex montana* L., *Cirsium decussatum* Janka, *Fallopia convolvulus* (L.) Á. Löve, *Filipendula vulgaris* Moench, *Hypericum perforatum* L., *Silene vulgaris* (Moench) Garcke, *S. viscaria* (L.) Jess., *Stachys officinalis* (L.) Trevis., *Veronica spuria* L. etc. appear. In addition, the species composition of other ecological-coenotic groups also expands: *Carex hirta* L., *C. lachenalii* Schkuhr, *Galeopsis bifida* Boenn are found in the moist meadow group; the group of nemoral plants is supplemented by *Euonymus europaeus* L., *Lathyrus niger* (L.) Bernh. and *Pyrus communis* L., and the group of forest-edge nitrophilous group – by *Galium*

aparine L. Apparently, this is due to the activity of animals, primarily birds, that use single trees like resting places and brought diaspores of these plants. It is known that birds actively disperse seeds of many plant species (Levina, 1957; Cramp, 1998, etc.). Thus, thanks to single trees, the polydominant composition of the community with maximum species diversity is maintained. However, shading has an adverse effect on the state of coenopopulations of model plant species.

Iris aphylla loses positions in the herb layer of polydominant steppe meadows with single generative trees. Population density is 50 plants per 1 m². This is almost twice as low as in polydominant steppe meadows. A decrease in density is explained by the fact that due to the small amount of light, very few fruiting individuals able to produce viable seeds are formed in *Iris aphylla*. This leads to a four-fold drop in the number of young seed plants in the coenopopulation. Established plants feature an increased area of the leaf blade (Table 2). This adaptation allows the plants to get more of the scattered light. However, due to the lack of light, most individuals of *Iris aphylla* develop only to the ν -ontogenetic state, and then die. As a result, an incomplete ontogenetic spectrum is formed with a maximum at ν plants (Figure 6, 1b). If, over time, the number of trees on the slope increases, and they form a close-canopy area of the forest, the coenopopulation of *Iris aphylla* will disappear.

Anthericum ramosum shows low cover in the herb layer of polydominant steppe meadows with single generative trees. Under the tree canopy, population density of *A. ramosum* decreases sharply and only reaches 7 plants per 1 m². This is eight times lower than in polydominant steppe meadows. Here, an unfinished left-hand type ontogenetic spectrum is formed with a maximum at ν and g_h individuals (Figure 6, 2b). There are no ss or s individuals in the coenopopulation, which is probably due to the death of plants already in the g_3 state. In addition, the decrease in the population density is explained by the fact that due to a small amount of light, the mortality of j and im individuals increases. The group of ν and g_h plants is replenished by

single temporarily not flowering generative plants and particles formed as a result of disintegration of g_2 plants. For the same reason, the number of g_3 individuals, which

are represented by branching and non-branching particles, increases slightly.

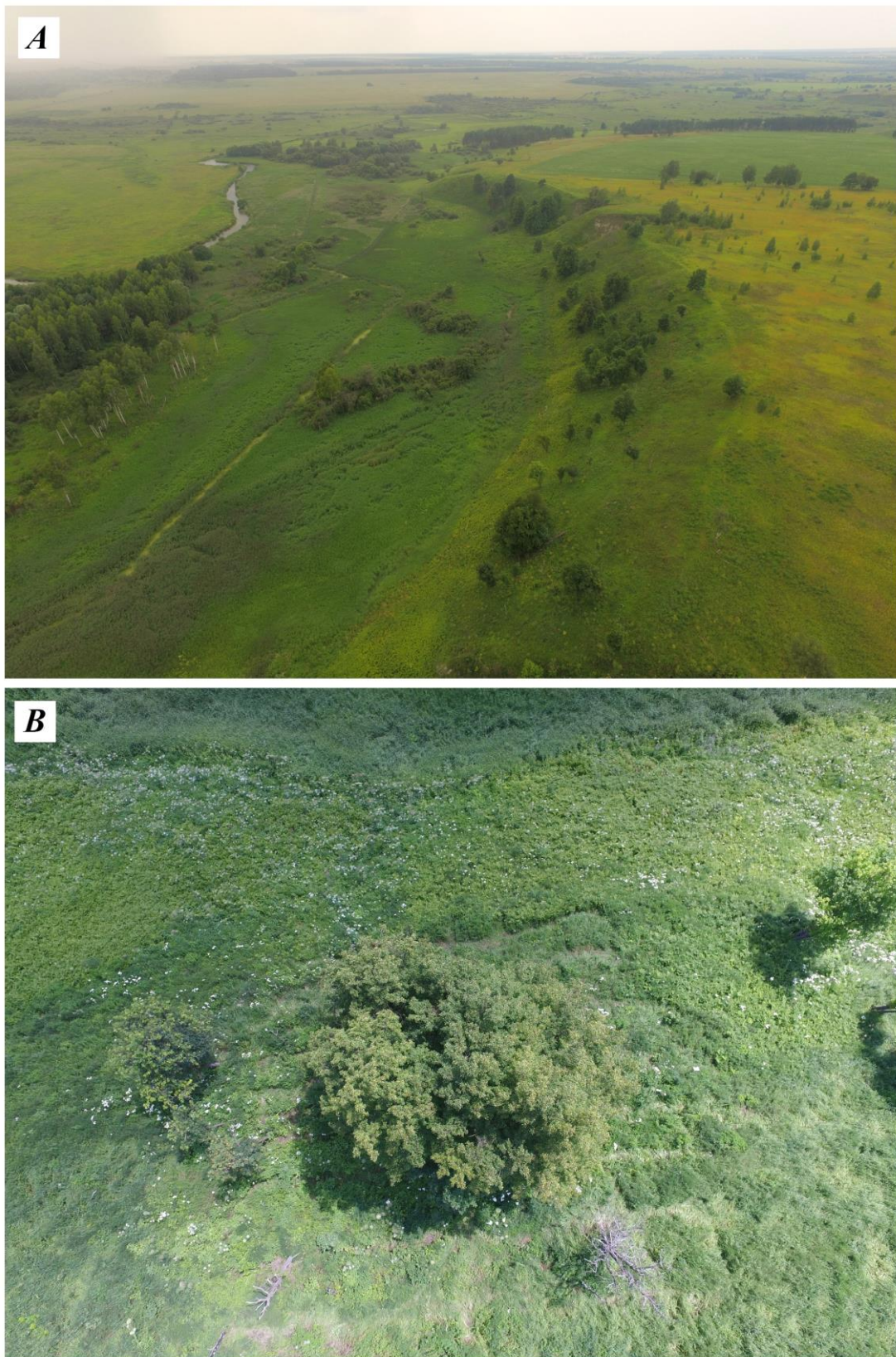


Figure 9. Polydominant steppe meadows with single trees: *A* – general appearance of the slope, *B* – crown of *Tilia cordata* from above. Photo by A.Yu. Sitnikov

Table 2. Length and width of the leaves of *Iris aphylla* in the light (1) and in the shade (2)

Measurement	<i>N</i>		<i>M</i> ± <i>m_M</i>		<i>σ</i>		<i>U</i>	
	1	2	1	2	1	2	1	2
Leaf length, cm	22	26	31.4 ± 2.22	60.6 ± 1.70	10.4	8.7	6 (<i>p</i> = 0.000000)	
Leaf width, cm	22	26	1.6 ± 0.09	2.3 ± 0.08	0.4	0.4	56 (<i>p</i> = 0.000002)	

Note. Communities: 1 – polydominant steppe meadows, 2 – polydominant steppe meadows with single generative trees. *N* – number of measurements, *M* – arithmetic mean, *m_M* – error of the arithmetic mean, *σ* – standard deviation, *U* – Mann–Whitney test values, *p* – probability of error. Significant differences in the *U* test are shown in bold.

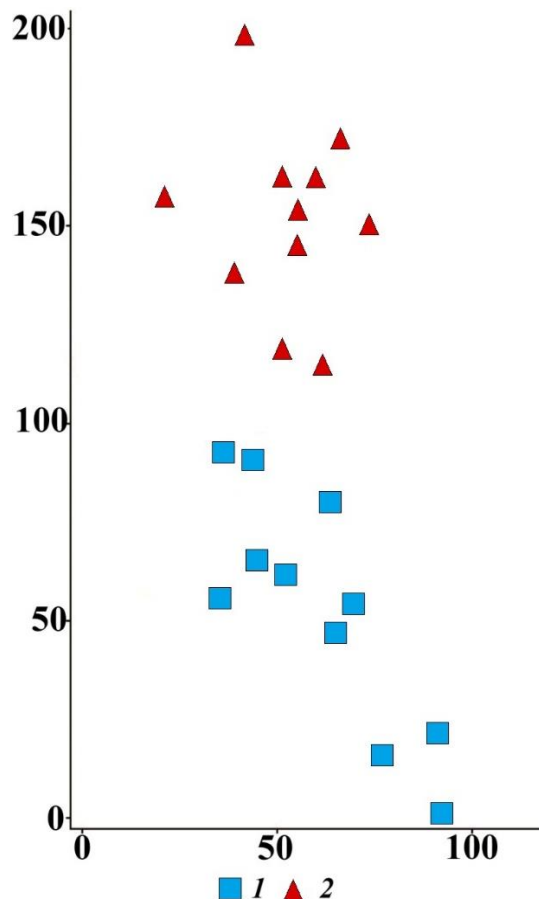


Figure 10. Results of DCA-ordination of relevés of steppe plant communities in the axes of the greatest variation in floristic composition. Communities: 1 – polydominant steppe meadows, 2 – polydominant steppe meadows with single generative trees

The projective cover of *Anemone sylvestris* is significantly less than in polydominant steppe meadows. Population density decreases six-fold – there are only 12 individuals per 1 m². In the shade, most anemones do not form flower stalks. Therefore, the generative fraction is represented by single fruiting individuals with predominant *g*₁ plants. They are mainly found

on the periphery of the crowns, where there is lateral illumination. As a result, the density of generative plants is ten times less than in the former community. This leads to a significant reduction in the replenishment of the coenopopulation with young plants, since the number of *g*₂ individuals that produce the largest number of root shoots decreases. Despite this, the ontogenetic spectrum of

Anemone sylvestris is still complete and left-hand type. However, it shows an extremely low participation of generative individuals and a shift of the maximum to v plants (Figure 6, 3b). The latter is due to the relatively long duration of the v -ontogenetic state and the insignificant replenishment of the coenopopulation by j and im plants.

CONCLUSION

The maximum species diversity of polydominant steppe meadows is maintained on steep slopes unsuitable for ploughing up, where haymaking and grazing are difficult and fires are infrequent. This contributes to the formation of stable coenopopulations of model species. Their ontogenetic spectra belong to one type – complete left-hand type, with the maximum accounted for by young individuals. The mechanism of formation of this spectrum is species-specific. Thus, individuals of *Iris aphylla* and *Anthericum ramosum* are characterized by vegetative reproduction with shallow rejuvenation of particles and frequent breaks in flowering. In addition, the left-hand type structure is provided by high seed productivity, and in case of *Anemone sylvestris* – by active vegetative reproduction, when plants are deeply rejuvenated. Single trees (*Quercus robur*, *Tilia cordata*) have controversial influence on the vegetation of polydominant

steppe meadows. On the one hand, with the introduction of trees, species diversity of communities increases. This is due to the fact that trees offer resting places and shelter for birds that spread plant diaspores. On the other hand, mature trees shade the herb cover. This leads to reduced cover and occurrence of steppe and dry meadow species, as well as affects their population structure. The number of individuals of all ontogenetic states is significantly reduced. The ontogenetic spectrum of *Anemone sylvestris* remains complete, whereas in *Iris aphylla* it becomes incomplete, and in *Anthericum ramosum* it becomes unfinished. If, over time, the number of trees on the slope increases, and they form a close-canopy area of the forest, coenopopulations of the model species will gradually disappear from the community.

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Species composition of the Melovitskie Slopes natural monument communities

Plant name	PO		ECG
	Communities		
	1	2	
<i>Achillea millefolium</i> L.	IV (+)	II (+)	D-Md
<i>Agrimonia eupatoria</i> L.	V (+)	IV(+)	D-Md
<i>Ajuga genevensis</i> L.	I (+)	I (+)	D-Md
<i>Allium oleraceum</i> L.	–	I (+)	D-Md
<i>Anemone sylvestris</i> L.	V (1)	II (1)	D-Md
<i>Anthericum ramosum</i> L.	V (1)	V (+)	D-Md
<i>Anthyllis vulneraria</i> L.	I (+)	–	D-Md
<i>Artemisia absinthium</i> L.	–	I (+)	D-Md
<i>Artemisia vulgaris</i> L.	–	II (+)	D-Md
<i>Asparagus officinalis</i> L.	I (+)	V (+)	D-Md
<i>Aster amellus</i> L.	V (3)	II (1)	D-Md
<i>Astragalus cicer</i> L.	IV (+)	V (1)	D-Md
<i>Astragalus glycyphyllos</i> L.	I (+)	IV (+)	D-Md
<i>Brachypodium pinnatum</i> (L.) Beauv.	II (2)	V (3)	Nm-FE
<i>Bromus inermis</i> Leyss.	V (3)	V (4)	D-Md
<i>Calamagrostis epigejos</i> (L.) Roth	IV (+)	V (1)	D-Md
<i>Campanula bononiensis</i> L.	V (+)	V (+)	D-Md
<i>Campanula rapunculoides</i> L.	II (+)	II (+)	D-Md
<i>Campanula sibirica</i> L.	II (+)	–	D-Md
<i>Carex hirta</i> L.	–	I (+)	M-Md
<i>Carex lachenalii</i> Schkuhr	–	IV (+)	M-Md
<i>Carex montana</i> L.	–	II (+)	D-Md
<i>Carex praecox</i> Schreb.	III (+)	IV (+)	D-Md
<i>Centaurea jacea</i> L.	III (+)	–	D-Md
<i>Centaurea phrygia</i> subsp. <i>pseudophrygia</i> (C.A. Mey.) Gugler	III (1)	II (+)	D-Md
<i>Chamaecytisus ruthenicus</i> (Fisch. ex Woloszcz.) Klaskova	V (+)	III (+)	D-Md
<i>Cichorium intybus</i> L.	I (+)	–	D-Md
<i>Cirsium decussatum</i> Janka	–	I (+)	D-Md
<i>Cirsium pannonicum</i> (L. fil.) Link	IV (1)	III (+)	D-Md
<i>Convallaria majalis</i> L.	IV (1)	IV (1)	Nm-Fo
<i>Convolvulus arvensis</i> L.	III (+)	V (+)	D-Md
<i>Corylus avellana</i> L.	IV (+)	V (+)	Nm-Fo
<i>Dactylis glomerata</i> L.	III (+)	V (+)	M-Md
<i>Elymus repens</i> (L.) Gould	II (+)	II (+)	D-Md
<i>Equisetum arvense</i> L.	–	I (+)	D-Md
<i>Erigeron annuus</i> (L.) Desf.	–	I (+)	D-Md
<i>Euonymus europaeus</i> L.	–	III (+)	Nm-Fo
<i>Euphorbia esula</i> L.	II (+)	I (+)	D-Md
<i>Euphorbia semivillosa</i> (Prokh.) Krylov	V (2)	V (+)	D-Md
<i>Fallopia convolvulus</i> (L.) Á. Löve	–	I (+)	D-Md
<i>Festuca pratensis</i> Huds.	II (+)	–	D-Md
<i>Filipendula vulgaris</i> Moench	–	IV (+)	D-Md

Plant name	PO		ECG
	Communities		
	1	2	
<i>Fragaria viridis</i> Weston	III (+)	III (+)	D-Md
<i>Frangula alnus</i> Mill.	IV (+)	II (+)	Br-Fo
<i>Galatella linosyris</i> (L.) Rchb.f.	II (+)	II (+)	D-Md
<i>Galeopsis bifida</i> Boenn.	–	III (+)	M-Md
<i>Galium aparine</i> L.	–	IV (+)	Nt-FE
<i>Galium boreale</i> L.	V (+)	V (1)	D-Md
<i>Galium mollugo</i> L.	V (1)	V (1)	M-Md
<i>Galium tinctorium</i> L.	V (1)	V (+)	D-Md
<i>Galium verum</i> L.	V (+)	V (+)	D-Md
<i>Genista tinctoria</i> L.	IV (+)	I (+)	D-Md
<i>Geranium sanguineum</i> L.	IV (+)	IV (+)	D-Md
<i>Hypericum perforatum</i> L.	I (+)	III (+)	D-Md
<i>Inula hirta</i> L.	II (1)	IV (+)	D-Md
<i>Inula salicina</i> L.	V (1)	V (+)	D-Md
<i>Iris aphylla</i> L.	V (3)	V (2)	D-Md
<i>Knautia arvensis</i> (L.) Coult.	III (+)	V (+)	D-Md
<i>Lactuca serriola</i> L.	–	I (+)	D-Md
<i>Laserpitium latifolium</i> L.	IV (1)	V (2)	Nm-FE
<i>Lathyrus niger</i> (L.) Bernh.	–	V (1)	Nm-Fo
<i>Lathyrus pisiformis</i> L.	I (+)	–	Nm-FE
<i>Lathyrus sylvestris</i> L.	II (+)	IV (1)	Nm-FE
<i>Lavatera thuringiaca</i> L.	I (+)	I (+)	D-Md
<i>Leucanthemum vulgare</i> (Vaill.) Lam.	IV (1)	I (+)	D-Md
<i>Linum flavum</i> L.	IV (+)	I (+)	D-Md
<i>Lithospermum officinale</i> L.	IV (+)	IV (+)	D-Md
<i>Medicago falcata</i> L.	I (+)	V (+)	D-Md
<i>Myosotis ramosissima</i> Rochel	–	I (+)	D-Md
<i>Nepeta nuda</i> L.	I (1)	IV (2)	D-Md
<i>Origanum vulgare</i> L.	IV (1)	V (1)	D-Md
<i>Peucedanum alsaticum</i> L.	V (1)	V (+)	D-Md
<i>Peucedanum cervaria</i> (L.) Cusson ex Lapeyr.	IV (1)	V (1)	Nm-FE
<i>Peucedanum oreoselinum</i> (L.) Moench	I (+)	–	D-Md
<i>Phlomidis tuberosa</i> (L.) Moench	II (+)	II (1)	D-Md
<i>Pilosella piloselloides</i> subsp. <i>bauhinii</i> (Schult.) S.Bräut. & Greuter	I (+)	–	D-Md
<i>Plantago lanceolata</i> L.	I (+)	–	D-Md
<i>Plantago media</i> L.	I (+)	–	D-Md
<i>Poa angustifolia</i> L.	V (1)	V (1)	D-Md
<i>Poa trivialis</i> L.	–	IV (+)	M-Md
<i>Podospermum purpureum</i> (L.) W.D.J. Koch & Ziz	I (+)	–	D-Md
<i>Polygala comosa</i> Schkuhr	III (+)	–	D-Md
<i>Polygonatum odoratum</i> (Mill.) Druce	III (+)	II (+)	D-Md
<i>Prunus cerasus</i> L.	IV (1)	III (+)	D-Md
<i>Pteridium aquilinum</i> (L.) Kuhn	IV (2)	V (2)	Pn
<i>Pyrethrum corymbosum</i> (L.) Scop.	V (1)	V (1)	Nm-FE

Plant name	PO		ECG
	Communities		
	1	2	
<i>Pyrus communis</i> L.	–	I (+)	Nm-Fo
<i>Quercus robur</i> L.	I (+)	V (+)	Nm-Fo
<i>Ranunculus polyanthemos</i> L.	IV (+)	I (+)	D-Md
<i>Rubus caesius</i> L.	II (+)	III (1)	Nt-FE
<i>Salvia pratensis</i> L.	V (3)	V (1)	D-Md
<i>Salvia verticillata</i> L.	II (+)	I (+)	D-Md
<i>Securigera varia</i> (L.) Lassen	IV (1)	V (1)	D-Md
<i>Sedum maximum</i> (L.) Suter	I (+)	–	D-Md
<i>Sedum telephium</i> L.	I (+)	–	D-Md
<i>Serratula tinctoria</i> L.	–	I (+)	Nm-FE
<i>Seseli libanotis</i> (L.) W.D.J. Koch	I (2)	III (+)	D-Md
<i>Silene latifolia</i> Poir.	I (+)	III (+)	D-Md
<i>Silene nutans</i> L.	I (+)	I (+)	D-Md
<i>Silene viscaria</i> (L.) Jess.	–	I (+)	D-Md
<i>Silene vulgaris</i> (Moench) Garcke	–	I (+)	D-Md
<i>Solidago virgaurea</i> L.	I (+)	III (+)	Pn
<i>Stachys officinalis</i> (L.) Trevis.	–	V (+)	D-Md
<i>Stachys recta</i> L.	V (3)	V (1)	D-Md
<i>Succisa pratensis</i> Moench	I (+)	–	M-Md
<i>Taraxacum officinale</i> Wigg.	II (+)	I (+)	D-Md
<i>Thalictrum lucidum</i> L.	III (+)	–	M-Md
<i>Thalictrum minus</i> L.	III (1)	III (+)	D-Md
<i>Tilia cordata</i> Mill.	–	IV (+)	Nm-Fo
<i>Tragopogon dubius</i> Scop.	I (+)	–	D-Md
<i>Trifolium alpestre</i> L.	V (1)	V (1)	D-Md
<i>Trifolium montanum</i> L.	V (+)	II (+)	D-Md
<i>Valeriana officinalis</i> L.	III (+)	II (+)	Nt-FE
<i>Verbascum lychnitis</i> L.	II (+)	I (+)	D-Md
<i>Verbascum nigrum</i> L.	V (+)	IV (+)	D-Md
<i>Veronica austriaca</i> subsp. <i>teucrium</i> (L.) D.A. Webb	V (1)	V (1)	D-Md
<i>Veronica chamaedrys</i> L.	–	I (+)	D-Md
<i>Veronica spuria</i> L.	–	I (+)	D-Md
<i>Vicia tenuifolia</i> Roth	V (2)	V (1)	D-Md
<i>Vicia tetrasperma</i> (L.) Schreb.	–	I (+)	M-Md
<i>Vincetoxicum hirundinaria</i> Medik.	V (1)	V (+)	D-Md
<i>Viola canina</i> L.	I (+)	–	M-Md
<i>Viola collina</i> Besser.	III (+)	IV (+)	Pn
<i>Viola hirta</i> L.	IV (+)	V (+)	D-Md
<i>Viola mirabilis</i> L.	I (+)	III (+)	Nm-Fo
Number of species	98	107	

Note. Communities: 1 – polydominant steppe meadows, 2 – polydominant steppe meadows with single generative trees
 PO – average occurrence points, Arabic numerals and «+» – points of cover-abundance scale proposed by J. Braun-Blanquet. ECG – ecological-coenotic groups: D-Md – dry meadow, M-Md – moist meadow, Pn – piny (boreal forest-edge), Nm-FE – nemoral forest edge, Nm-Fo – nemoral forest, Nt-FE – nitrophilous forest-edge, Br-Fo – boreal forest.